Designer crops: optimal root system architecture for nutrient acquisition

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Plant root systems are highly plastic in response to environmental stimuli. Improved nutrient acquisition can increase fertilizer use efficiency and is critical for crop production. Recent analyses of field-grown crops highlighted the importance of root system architecture (RSA) in nutrient acquisition. This indicated that it is feasible in practice to exploit genotypes or mutations giving rise to optimal RSA for crop design in the future, especially with respect to plant breeding for infertile soils.

Root growth plasticity

RSA plays important roles in a range of processes throughout plant life cycles, such as anchorage and nutrient and water acquisition. Generally, root systems can be divided into a tap root system and a fibrous root system depending on their morphological and anatomical organization [1]. Dicots, such as the model plant *Arabidopsis thaliana* and the crop *Brassica rapa*, mainly form a tap root system comprising a single embryonically initiated primary root (PR) and post-embryonically initiated lateral roots (LRs). By contrast, most monocot crops, including wheat, rice, and maize, have a fibrous root system comprising of embryonic PRs and seminal roots (SRs), and post-embryonic shoot-borne roots and LRs [2,3].

The structure of the root system is not only shaped by endogenous genetic programs, but is also greatly influenced by environmental cues [4]. Water and soil nutrients including nitrogen (N) and phosphorus (P), which are critical elements that limit the growth and yield of diverse crops including maize, can strongly change RSA depending on their availability [5,6].

Nitrate (mobile soil resources)

Nitrate rather than ammonium is the major source of N in many crop production environments [6]. Nitrate is highly soluble in soil solution and can be lost easily. In crops, especially maize, the crown root (CR) is the most important part of the root system for soil resource acquisition during vegetative growth and remains important through reproductive development; while in *A. thaliana* and *B. rapa*, the PR and its LRs remain dominant [2,7]. In *Arabidopsis*, LR elongation is significantly stimulated in low nitrate conditions [8,9]. By contrast, PR length remains constant across a range of nitrate concentrations. These observations suggest that the differential growth dynamics of a root system may be crucial for plants to adapt to certain growth conditions. Currently, RSA research in cereals has mainly focused on rice and maize. Recently, using an aeroponics system for maize, Gaudin *et al.* demonstrated that low nitrate dramatically increased the individual CR elongation and was accompanied by a decrease in CR density in adult maize. However, low nitrate caused an increase in the length and the density of the first-order and second-order LRs, whereas low nitrate reduced root hair length and density [10]. Consistently, Saengwilai *et al.* reported that maize responds to N limitation by increasing the length of CRs while reducing CR whorl number and CR number per whorl, and provided evidence that maize genotypes with low CR number confer N acquisition from low nitrate soils through enhancing deep soil exploration and decreasing competition among CRs in low nitrate in the field [11] (Figure 1). More recently, Postma *et al.* showed that maize genotypes with low LR branching density but longer LRs increased nitrate uptake by reduced root competition and increased soil exploration [12]. These results indicate that steeper and longer RSA is an important strategy for nitrogen acquisition in deeper soil, where mobile resources such as water and sulfate are more available (Figure 1).

Phosphorus (immobile soil resources)

More and more evidence indicates that PR and LR growth is restrained in low phosphate conditions – likely due to reduced meristem activity – while LR density is stimulated in many species including *A. thaliana* and rice [6,8]. In addition, root hair development is also stimulated in response to low phosphate [6]. These results suggest that the effect of low phosphate on RSA is opposite to that of low nitrate. Consistent with these, maize genotypes with high LR branching density but shorter LRs were optimal for phosphorus acquisition, and the increased LR branching density does not increase root competition [12]. In addition, in rice, overexpression of PHOSPHORUS-STARVATION

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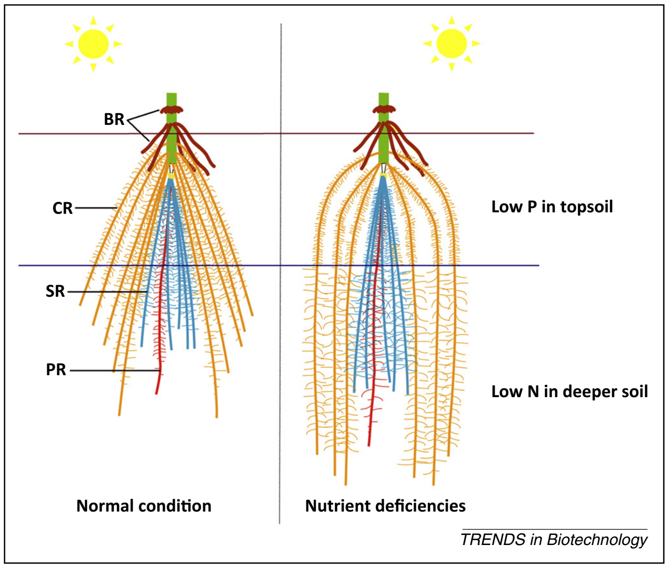

Figure 1. The optimal adult maize root system architecture for N and P acquisition. Abbreviations: BR, brace root; CR, crown root; PR, primary root; SR, seminal root.

TOLERANCE 1 (*PSTOL1*) enhanced grain yield and increased P acquisition in P-deficient soil through regulation of RSA [13]. Taken together, these observations indicate that shallower and shorter root architecture with more branches is a good trait for immobile resource acquisition such as phosphorus, potassium, iron, and manganese in topsoil (Figure 1).

Concluding remarks and future perspectives

One of the challenges of modern agriculture is the improvement of crop nutrient acquisition under changing environmental conditions. Plants are highly plastic and adapted to diverse growth conditions such as nutrient deficiencies in soils by modifying RSA. Thus, RSA is an important trait for genetic improvement of nutrient acquisition from nutrient-limiting soils. Recently, several studies demonstrated that plant RSA was profoundly affected not only by nutrient availability but also by other environmental cues such as salt, light, and aluminum toxicity [4,14]. This plasticity in RSA is regulated by plant hormones; for example, ABA and auxin regulate the differential growth dynamics between PRs and LRs in responses to salt stress or nitrate availability [5,15].

In rice, *DEEPER ROOTING 1* (*DRO1*) is expected to enhance grain yield under drought conditions by altering RSA [16]. Therefore, based on the recent studies in rice and maize, it is feasible in practice to exploit optimal RSA as an effective strategy to improve crop stress tolerance and yield under exacerbated climate change. One major challenge will be to reconcile the optimal root architectures for, for example, N and P acquisition in one root system. However, there is a tradeoff between the nitrate and phosphate acquisition efficiency depending on their relative availability in the field. Especially since the optimal RSA is also related to the carbon status of the plant, planting density, and air temperature [12], computer modeling will be a helpful tool to design the optimal RSA for nutrient acquisition. Furthermore, the use of cell- or tissue-specific promoters to control the branching density and root length will overcome this challenge [15].

In depth characterization of RSA and underlying molecular mechanisms directly in crops using novel approaches, such as X-ray μ-computed tomography on soil-grown roots [17,18], in parallel with translating RSA knowledge from the model plant *Arabidopsis* into crops will address some of the challenges agriculture is facing.

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